


Article

Feeding Specialization of Honey Badgers in the Sahara Desert: A Trial of Life in a Hard Environment

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Abstract: The honey badger (*Mellivora capensis*) is a medium-sized carnivore distributed throughout Africa to the Arabian Peninsula, Iran, Turkmenistan, and India. However, available information on its ecology is very scarce. We studied its feeding ecology in the remote north-western Sahara Desert, based on the contents of 125 fecal samples collected during large scale surveys. Samples were confirmed to belong to honey badgers by camera trapping and genetic analyses. Barely 18 prey species were detected. The diet primarily consisted of spiny-tailed lizards *Uromastix nigriventris* and *U. dispar* (72% of volume in scats). Secondary prey items were arthropods (14%), small mammals (8%), other reptiles (4%), and eggs (0.8%). Some small geographic and temporal differences were related to the consumption of beetle larvae and rodents as alternative prey. Camera trapping and distance sampling surveys showed that diel activities did not overlap between honey badgers and spiny-tailed lizards, suggesting that badgers primarily dig lizards out of their burrows when inactive. Consumption of spiny lizards by other sympatric meso-carnivores was < 6.1% of occurrence (223 analyzed scats); the honey badger behaved as a trophic specialist in the Sahara, probably thanks to exclusive anatomical adaptations for digging. We discuss the role of this circumstance minimizing the exploitative competition, which could allow the survival of this large mustelid in this low productive and highly competitive environment.

Keywords: arid environments; exploitative competence; specialist; feeding ecology; *Mellivora capensis*; Sahara; *Uromastix* genus

1. Introduction

The largest desert in the World, the Sahara (9.2 million km²; almost the area of Europe, 10.2 km²), has a surprising rich community of mammalian carnivores with up to 14 species after excluding some recently extinct taxa (lion *Panthera leo* and wild dog *Lycaon pictus* [1,2]). However, basic information on the biology of many species in the Sahara remains mostly unknown, primarily due to both severe logistic limitations and political conflicts, which imply the lack of security for researchers in several areas [3,4]. One of these carnivores is the honey badger (*Mellivora capensis*), a large mustelid widespread through most of Africa to the Arabian Peninsula, Iran, Turkmenistan, and the India sub-continent, including the western Sahara Desert, from Mauritania and Mali to southern Morocco and north-western Algeria [1,5]. However, detailed studies of honey badger ecology are limited to southern Africa [6,7], and only opportunistic observations scattered in the Sahara Desert are available [5,8,9]. Any aspect of its biology in the extreme habitats of the Sahara (as well as other areas) remain poorly understood. On the other hand, the North-western Sahara range of the honey badger is located in the Northern distribution range of the species in Africa, which represents biogeographic interest where severe ecological limitations are predictable. Moreover, recent species distribution models suggest that the honey badgers of NW Sahara could be currently isolated from the rest of African populations [10].

Honey badgers capture most of their prey by digging with powerful and broad front feet and long claws [5], preying mostly on small burrowing vertebrates and insects and, secondarily, roots, berries, and fruits [1,5–9]. On the other hand, the richness (or diversity) of the Saharan carnivore community in the very low productive Saharan eco-region [1,2,11] implies a highly competitive scenario, where strong niche partitioning is expected following the competitive exclusion principle [12]. Here, we present the first detailed information on the feeding ecology of the honey badger in the Sahara Desert, based on the analysis of fecal samples collected during large scale surveys carried out in remote areas of the Sahara. We hypothesized honey badgers to lower exploitative competition by preying primarily upon small burrowing vertebrates and insects only marginally used by other sympatric carnivore species. We assessed the diel activity of badgers and other mesocarnivores' diets to test for this hypothesis. This is an interesting scenario to study the adaptations and or conditions that allow the survival of isolated populations living in marginal habitats. In fact, key local adaptations in the feeding ecology of marginal and or isolated populations can lead to allopatric speciation, being an important driver of evolution [13]. Further, from a conservation point of view, as the honey badger is a near-threatened taxa in the Maghreb countries [14], this information contributes to correctly designed conservation strategies. This is a key goal to face the severe crisis that currently affects the rich wildlife of the Sahara, where much more scientific attention is required [2,3].

2. Materials and Methods

2.1. Study Area

The study area was in the Atlantic Sahara (Morocco), a low-latitude subtropical desert with arid hot climate (after Köppen-Geiger classification, [15], where the mean temperature ranges from 22.7 °C in the west (closer to the Atlantic Ocean) to 23.2 °C in the eastern inland areas, and total annual precipitation ranges from 138 to 59 mm, respectively (climate stations at Smara: 26°46'N, 11°31'W, 460 m and Tindouf: 27°40'N, 8°7'W, 401 m). Three areas were surveyed for the present study. The first one was located between the lower Draa River and the upper basin of the Sequiat Al Hamra, (ca km²; altitude ranges 290–770 m a.s.l.; Figure 1). It is a hilly and rocky terrain with intercalated hamadas (elevated plains) and regs (gravels/stony plains). A complex network of ancient dry rivers crosses the entire region, some of them collecting seasonal waters and even the main basins, while the main rivers, the Draa and the Chebeica, hold some permanent water pools, called *gueltas*. The vegetation is scarce except in the dry rivers basins, where large open savannah-like forests of horn trees (*Acacia raddiana*) persist, somewhere with Egyptian balsam (*Balanites aegyptiaca*) and Sodom apple (*Calotropis procera*) and *Rhus tripartita* bushes, while tamarisk (*Tamarix africana*) grows near the *gueltas*. The endemic tree

of Morocco, the argan (*Argania spinosa*), reaches its southernmost limit here as scattered individuals sheltered in the valleys. The second area comprises the Oued Khat basin (Figure 1), a fossil river valley dominated by reg plains with rocky hills and steps at the borders (ca 1200 km², 110–220 m a.s.l.). The vegetation is formed by scattered horn trees and camephites as *Nucularia perrini*. The third area includes the Negjyr Mounts, the Aouserd Mounts and the Oued Jenna (Figure 1), which conform small island-mounts (6–80 km²) and an ancient dry river located in the huge Atlantic Saharan plain (ca 5100 km², 180–350 m a.s.l.). Climate and vegetation are similar to the Oued Khat area, but the grass *Panicum turgidum* is more widespread.

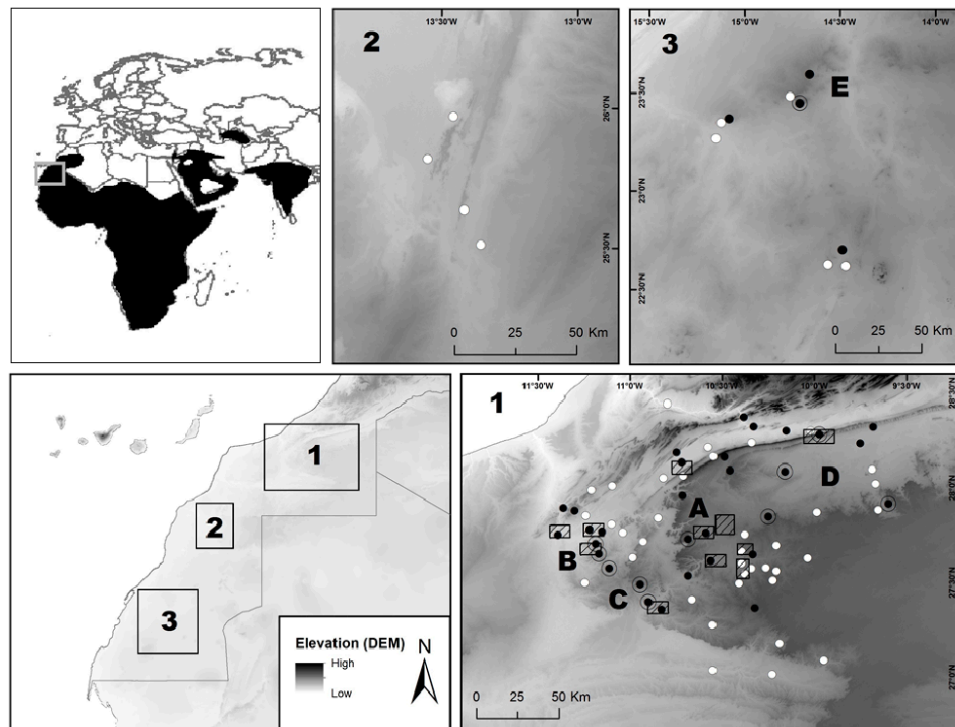


Figure 1. Study areas in the Atlantic Sahara (from 2013 ESRI, i-cube, GeoEye), honey badger global range [14] and distribution of the walking survey plots: Black points are sites where honey badgers were detected (feces, footprints, camera trap records and sightings) and white points are negative surveys; encircled black points show where the honey badger feces were collected: A) Red Aydar, B) Black Aydar N, C) Black Aydar SE, D) Tigsert Basin, E) Negjyr. Rectangles show the camera trapping sites.

Currently, the carnivore mammals community of the Atlantic Sahara is formed by 12 species belonging to 6 families [11]: 4 canids (African golden wolf *Canis anthus*, red fox *Vulpes vulpes*, Ruppell's fox *V. rueppellii*, fenec fox *V. zerda*), 3 felids (caracal *Caracal caracal*, African wildcat *Felis lybica*, sand cat *F. margarita*), 2 mustelids (honey badger and Saharan striped weasel *Poecilistis libyca*), 1 viverrid (common genet *Genetta genetta*), 1 herpestid (Egyptian mongoose *Herpestes ichneumon*) and 1 hyenid (striped hyaena *Hyanea hyanea*). We failed to detect cheetahs (*Acinonix jubatus*), which probably became extinct at the end of the 20th century [11].

2.2. Field Surveys

We monitored the carnivore community of the 3 study areas during 22 expeditions of 1 to 2 weeks each (from April 2011 to April 2019). A total of 68, 4, and 9 plots were, respectively, sampled within the 3 areas (Figure 1), searching for carnivore's signs along 1–4 transects (mean length: 12.08 ± 0.72 km per walking survey, for a total of 2.490 km accumulated effort). During each walking survey, 2 to 9 observers searched for carnivore feces, tracks, and den sites [16,17], following a stratified sampling strategy within the available habitats in each sampling point.

2.3. Feces Identification

The honey badger feces can be confused with those feces of similarly sized sympatric carnivore species (African golden wolf, red fox, and African wildcat). In the field, scats were preliminarily assigned to the honey badger whenever other signs of presence, such as tracks and hairs, were found. Then, we employed camera trapping at the first found den (Red Aydar, April 2014, Figure 1) for positive species identification [18]. Two passive infra-red triggered cameras were set relatively close (10 m) and just in front one of the den entrances for 5 days with bee honey as a lure. Two males honey badgers were photographed on 2 different days (Figure 2) and no other carnivore species were detected. This would confirm that the 38 scats (see Table 1) found next to the den probably belonged to honey badgers



Figure 2. A picture of the first honey badgers taken by a camera-trap in our study, showing the typical micro-habitat where this species shelters in the study area. The entrance of the den (not visible in the picture) was located just to the left of the left-most individual.

We used laboratory confirmation by DNA isolation and identification. First, we extracted the DNA of 223 carnivore feces collected everywhere during the walking surveys, which were identified at species level. Second, we extracted the DNA of a sub-sample of 28 out of 119 feces found around dens and in latrines, including 10 samples of the camera-surveyed den previously described; these 119 samples were in situ identified as honey badger scats, following shape, size, and location criteria, once we learnt from the scats that could be identified by camera trapping. All samples were handled in an isolated, dedicated low-quality DNA laboratory, which was cleaned with bleach and irradiated between each reaction. Mitochondrial DNA was extracted from the feces with the QIAamp DNA Stool Kit (Qiagen, Hilden, Germany), using phenol-chloroform-isoamyl alcohol (PCI; [19]), or by silica [20], using a negative extraction control for every 5 samples.

Two PCRs targeting a 280 bp fragment of the *cyt b* were carried out per extract and negative with primers cCB53 5'-CCTATTCTAGCCATACACTACA [21] and uCB54 5'-AAGGATATTGGCCTCATGG [22]. PCR negatives were included in each batch. Each 12 µL reaction contained 1U GoldTaq polymerase®, 1X GoldTaq Buffer®, 2.5 mM MgCl₂, 1 mM dNTP, 0.4 mM BSA, 0.5 µM each primer, and 3 µL of DNA extract. Cycling was carried out in a BioRad T100 thermocycler, with initial denaturation at 95 °C for 8'; we ran 45 cycles of 95 °C for 30'', 55 °C for 30'', 72 °C for 60'', with a final extension at 72 °C for 7'. Products were checked in a 2% agarose gel and visualized on a Gel Doc™ EZ Gel transilluminator (Bio Rad, Hercules, CA, USA). PCR products

were purified using Sera Mag SPRI beads [23] and checked by agarose gel electrophoresis and Sanger sequenced (Macrogen, Madrid, Spain).

We trimmed primer and low-quality base pairs from the sequences and BLASTed them against the GenBank database using the blastn algorithm [24] implemented in Geneious v11.0.5 [25]. Sequence identity was approximated by similarity in the whole database and then confirmed by phylogenetic analyses. Reference sequences from all carnivores present in the region were obtained from GenBank and a neighbor-joining phylogeny was constructed in Geneious with default parameters. Twenty-three of the selected 28 feces were successfully amplified and sequenced, 14 in duplicate. All were positively identified as honey badger through similarity and phylogenetic analyses. Therefore, the identification success ratio of feces identified in situ (samples found around dens and latrines) was 100%. Of the 223 feces collected during the carnivore surveys, 6 belonged to the honey badger. In total, we obtained 125 confirmed feces.

2.4. Faecal Analysis and Diet Composition

The scats, previously dry-preserved with silica-gel, were broken up and the prey remains were identified to species, where possible, based on macroscopic characteristics of bones, hairs, reptile scales, and invertebrates pieces compared with the reference personal material of collection, bibliography (rodent teeth: [11]) or were consulted to specialists (Coleoptera Order). The percentage of the volume of each identified prey per scat was estimated visually [26,27]. The composition of the diet was expressed as a percentage of volume (%V = estimated volume of each prey type/total estimated volume \times 100). In order to study regional variations in diet, the samples were separated into 5 areas (Figure 1). Seasonal and/or inter-annual variations could be studied only for one area (Red Aydar, see Figure 1) due to sampling size limitations; the samples obtained in this area during 2 visits were considered separately (see Table 1). Food items were grouped into 5 categories: Spiny-tailed lizard, other reptiles, small mammals, eggs and arthropods. Kruskal-Wallis's tests were used to detect overall differences in the diet for each one of the 5 categories, whereas Mann-Whitney's U tests were used to detect differences for each category between pairwise areas/seasons. The sample of Negjyr (< 10 scats, Table 1) was excluded from U tests.

Table 1. The occurrence of the prey species in the honey badger feces (feces in which each item was found).

Food Item	Red Aydar Apr.2014	Red Aydar Dec. 2016	Black Aydar SE Apr.2014 & Dec. 2016	Black Aydar N Dec 2016	Tigsert Basin 2012–2019	Negjyr Jan. 2015
<i>Uromastix nigriventris</i>	30	9	18	15	10	0
<i>U. dispar</i>	0	0	0	0	0	6
<i>Agama sp./Trapelus sp.</i>	1	0	2	1	1	0
Snake n.i.	1	1	1	0	0	0
<i>Lepus sp.</i>	1	0	0	0	0	0
<i>Atlantoxerus getullus</i>	0	0	0	1	0	0
<i>Gerbillus campestris</i>	0	0	0	4	0	0
<i>Psammomys obesus</i>	0	2	0	4	0	0
<i>Acomys cahirinus</i>	0	1	0	0	0	0
Rodentia n.i.	0	1	1	1	0	0
<i>Alectoris barbara</i> eggs	1	0	0	0	0	0
Reptile eggs	1	0	2	0	0	0
Melolonthidae adults	8	1	1	0	0	0
Melolonthidae larvae	18	11	1	0	0	0
Tenebridae	0	3	0	0	0	0
Scorpion	0	1	0	0	0	0
Scolopendra	1	0	0	0	0	0
Arthropod n.i.	1	0	0	0	0	0
Lepidoptera pupae	0	0	1	0	0	0
Mud	1	0	0	0	0	0
N	38 scats	25 scats	23 scats	22 scats	11 scats	6 scats

2.5. Predator-Prey Relationships: Abundance and Diel Activity of the Staple prey

In order to know how abundant the staple prey was, data on the density of spiny-tailed lizard *Uromastix nigriventris* was estimated by distance sampling [28] by counting from vehicles. Samplings ($N = 4$) were carried out in late summer (25–26 September 2018), when lizards were active ([29]; this study) and thus should be recorded effectively. Transects were stratified by the 3 major habitats of the study area: Gravels/sandy reg (one transect of 32.49 km), stony reg (two transect of 27.01 and 20.0 km) and rocky hills (one transect of 8.38 km); given to the great homogeneity within these habitats, we assumed that our car surveys (87.88 km in total) were representative of the entire study area. During the surveys, one car was slowly driven (< 10 km/h) and two observers (not the driver) counted the individuals, one on each side of the route, taking the perpendicular distance (in m) to the survey line of each observation by rangefinder. The program *DISTANCE* 6.0 [30] was used to calculate density (D). The detection function was half-normal, since: (1) Data set allowed for neither uniform nor hazard-rate functions, (2) the half-normal function resulted in lower AIC values than the negative exponential function.

We explored whether the diel activity of the honey badger was shaped by the activity of its staple prey. *U. nigriventris* is a strictly diurnal species [29] that in the study area can be observed out of its burrows from 1 h after sunrise to 1 h before sunset (this study). Honey badger diel activity was estimated by camera trapping. Eleven surveys (Figure 1) with 3 to 24 cameras each (passive infrared triggered) were carried out since 2012 to 2019. Cameras were deployed for periods lasting five days to one year, totalling camera days for 159 effective cameras (some devices were stolen). We used digital passive infrared-triggered devices, baited at 3–6 m with Iberian lynx (*Lynx pardinus*) urine [31]. The date and time of each photograph were recorded. The diel activity pattern of honey badgers was assessed following Monterroso et al. [32], using Kernel density estimates (see details in [33]). All captures were separated >1 day, hence, they can be assumed as independent [18]. Very few pictures of lizards were obtained, insufficient for any activity analysis. We carried out the diel calculation by R [34], following the code provided by Ridout and Linkie [33].

2.6. Role of Staple Prey of Honey Badger in the Diet of Other Sympatric Carnivores

We studied the consumption of the staple prey of honey badgers by other carnivores living within the study area, with the aim of testing our hypothesis of niche segregation. The 223 identified carnivore feces were analyzed in detail to detect remains of the spiny-tailed lizard. We analyzed 80 samples belonging to African golden wolf, 37 to the red fox, 92 to the African wildcat, 7 of the Ruppell's fox, 3 of the fenec fox, 2 of the genet and 2 of the striped hyena.

3. Results

We were able to obtain 119 feces from the first area and 6 from the third area, failing to find any sample in the second area (see Figure 1). Within the first area, two occupied honey badger dens were discovered in April 2014, which held several scats around; in December 2016, we found three latrines containing honey badger-like feces. All these samples were collected and confirmed to belong to the target species, being resampled up to four times in following expeditions in order to obtain temporal variability in the sample.

The diet included 18 identified species (Table 1). Overall, there were only three key prey items: Spiny-tailed lizards (72.0 of average %V), arthropods, mainly larvae of one unidentified species of Melolonthidae (Coleoptera) (14.4% of average V) and rodents (8.5 of average %V). However, the importance of arthropods and rodents was local, whereas spiny-tailed lizards showed a key role in all the studied areas (Figure 3). No plant material was found in the samples. Statistical differences were found in the complete sample for the spiny-tailed lizard (K-W $\chi^2 = 15.17$, $f.d. = 5$, $P = 0.01$), small mammals (K-W $\chi^2 = 29.49$, $f.d. = 5$, $P < 0.0001$) and arthropods (K-W $\chi^2 = 53.90$, $f.d. = 5$, $P < 0.0001$). Some differences were detected by the pairwise comparisons, which were related to the

consumption patterns of spiny-tailed lizards and Melolonthidae larvae in Red Aydar and rodents in North Black Aydar (Table 2).

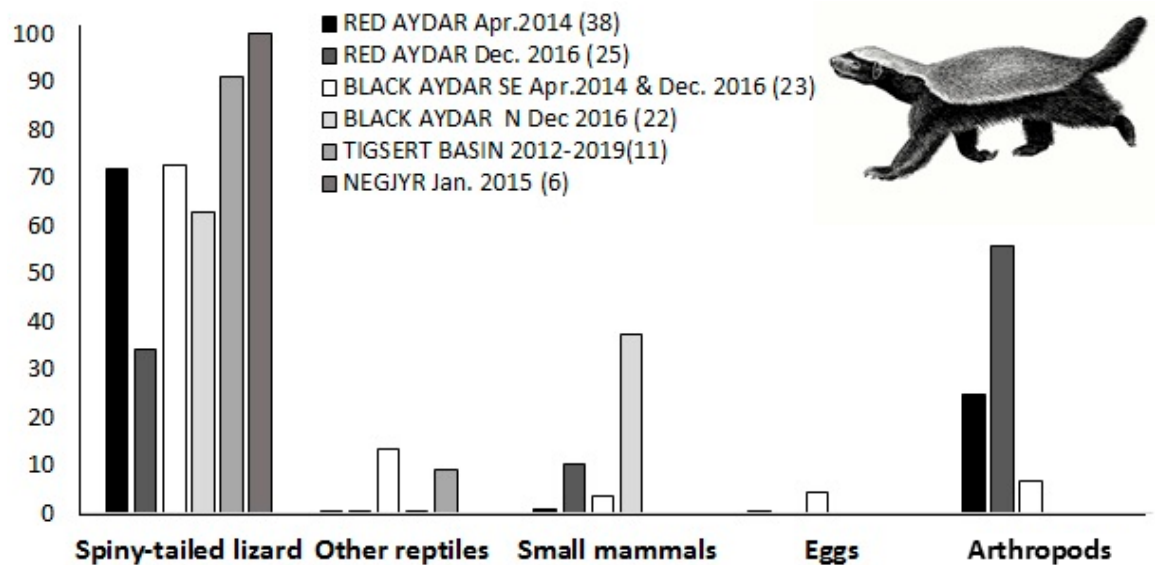


Figure 3. Diet of the honey badger in the Atlantic Sahara expressed as a percentage of volume in the scats. In () number of feces.

Table 2. Results of Mann-Whitney's pairwise tests (*P* values corrected by the Holm-Bonferroni adjustment) between areas/seasons.

Spiny-Tailed Lizard				
	Red Aydar Apr. 2016	Red Aydar Dec. 2014	Black Aydar SE	Tigsert Basin
Red Aydar Apr. 2014	-	-	-	-
Red Aydar Dec. 2016	n.s.	-	-	-
Black Aydar SE	n.s.	0.0001	-	-
Black Aydar N	n.s.	n.s.	n.s.	-
Tigsert basin	0.005	0.001	n.s.	n.s.
Melolonthidae				
Red Aydar Apr. 2014	-	-	-	-
Red Aydar Dec. 2014	n.s.	-	-	-
Black Aydar SE	0.001	0.001	-	-
Black Aydar N	0.0001	0.0001	n.s.	-
Tigsert basin	0.006	0.009	n.s.	n.s.
Small Mammals				
Red Aydar Apr. 2014	-	-	-	-
Red Aydar Dec. 2016	n.s.	-	-	-
Black Aydar SE	n.s.	n.s.	-	-
Black Aydar N	0.0001	n.s.	0.001	-
Tigsert basin	n.s.	n.s.	n.s.	n.s.

The estimated density of the spiny-lizard was 1.89 individuals/km² (SE = 1.36), excluding the gravel/sandy regs, since the presence was anecdotic (only one record). The number of records were insufficient to estimate the density within each habitat, but the relative abundance was highly variable: 0.03 individuals/km in gravel/sandy regs, 0.14–0.20 individuals/km in stony regs and 1.55 individuals/km in rocky hills. The honey badger was active mostly at night (23 out of 27 remote camera captures, 85.2%; see Figure 4).

We detected spiny-tailed lizard remains in 5 feces of African golden wolf (6.1%), 4 of African wildcat (4.3%) and in 1 of the red fox (2.7%).

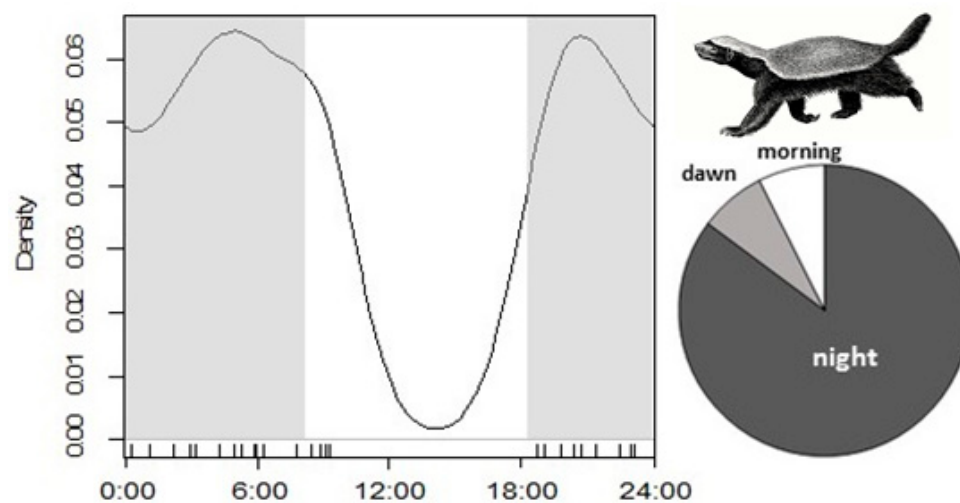


Figure 4. Activity patterns of the honey badger in the Atlantic Sahara. Darkness hours are indicated by the shaded area. Short vertical lines above the x-axis represent the 27 independent records. The pie chart represents these 27 records.

4. Discussion

Our hypothesis that honey badgers prey primarily upon small burrowing vertebrates and insects was fulfilled, showing a particular trophic specialization in the study area. The observed diet was much less diverse than that described in the most detailed honey badger study, which was conducted in Kgalagadi Transfrontier Park (South Africa and Botswana); Kgalagadi is a semi-arid southern African savannah (200–250 mm annual rainfall), where at least 59 species were consumed, with gerbils, geckos, and bee larvae the most frequently consumed items, whereas snakes and springhares were the most important in terms of biomass [7]. Another earlier study carried out in the same area showed that honey badgers ate mostly rodents, lizards, and scorpions [6]. The lesser diverse diet we observed in the north-western Sahara was expected since the Kgalagadi is a more productive environment than the Atlantic Sahara. Anyway, potential prey richness within our study area seems to be somewhat high: We have documented 9 snake species, 14 geckos and lizards, 2 hares, 5 large rodents, 8 small rodents (see also references [35] and [11]), and scorpions are really abundant. Although it is clear that availability estimations of potential prey are necessary for a wider discussion on food selection patterns, our data suggest that the honey badger could behave in the Sahara like a specialist, thus as the European badger *Meles meles* and earthworms in NW Europe [36]. Honey badgers were focused on the spiny-tailed lizard, which could be actively searched in the burrows even during its inactivity season (that lasts 5–6 months, from November to April, obs. of authors) or during its nocturnal resting period. The diel activity of the predator and prey do not overlap, but badgers probably find it easier to catch lizards in their burrows when inactive. The spiny-tailed lizard is a prey species that bears most of the characteristics to become a largely profitable food, as optimal foraging theory predicts [37]: It is locally abundant (in the rocky areas), with an apparent optimal size/weight for honey badgers (up to 0.6 kg [38]) and is probably easy for badgers to dig them out from their burrows, a local behavior previously described by Valverde [8]. Actually, it is well known that honey badgers capture most of their prey by digging [5].

Some plasticity in the honey badger diet may be suggested, probably related to changes in the availability of the Melolonthidae larvae and rodents, likely attributed to a short-term foraging response, as has been observed in other badger species (e.g., *Meles meles* and earthworms or rabbits, [39,40]). Spiny-tailed lizards are long-living reptiles well adapted to the extreme conditions of the Sahara Desert [41], therefore, it is not expected to suffer great temporal variations or short-term numerical responses like rodents or insects.

The name “honey badger” was given due to the famous taste of this mustelid for bee honey [5]. The observed absence of bee remains in the collected samples might be due to low local availability, as no bee nests were found during the field walking surveys. However, honey badger attack hives in some areas of the near Anti-Atlas range of Morocco, generating a conflict with beekeepers that generate illegal lethal control [42]. Watermelons (*Citrullus lanatus*) play some marginal role in the diet of the honey badger in the Kalahari Desert [7]. Similar watermelons (*C. colocynthis*) are abundant in our study area, however, it was not found in the scats and we failed to detect tracks around several plants. The fruits of the Egyptian balsam were cited as consumed by the species in the Air, Sahara of Niger [9], but were not detected in the diet in our study.

Although we recognize that further studies are necessary to assess the role of intra-guild competition in the carnivore community of the Atlantic Sahara, our results support the niche partitioning hypothesis. Carnivore species can coexist within a community by lowering interspecific competition [43]. Separation of trophic niche can be an efficient way to achieve coexistence (e.g., [44,45]). In our community, this coexistence was favored by honey badger specialization on the spiny-tailed lizard. The spiny-tailed lizard is difficult to capture by other carnivores than honey badgers due to: (1) This reptile usually burrows their dens in hard soils (obs. of authors) and (2) all carnivore species are primarily nocturnal here (data from our camera trapping survey). Thus, an optimal prey in terms of biomass remains available almost entirely for honey badgers within the carnivore mammal’s community, which probably plays a key-role for the survival of the northern-most populations of Africa.

Our study highlighted some interesting adaptations of this large mustelid to the arid scenario of the Sahara Desert that deserves more in-depth studies. For further research on honey badger distribution and ecology within this remote region where rocky soils prevent the finding of tracks, we recommend searching for scats at den sites similar to those described, all located at relatively predictable rocky slopes.

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